

Diet, Feeding Habits, Digestion, and Consumption in Sharks, with Special Reference to the Lemon Shark, *Negaprion brevirostris*

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ABSTRACT

Though the diets of many species of sharks have been described, little information exists about patterns of food intake and about the fate of prey items once they are ingested. Digestive physiology and efficiency of elasmobranchs are generally accepted as similar to those of teleosts, although digestive morphologies of the two groups differ. The lemon shark, *Negaprion brevirostris*, has been the subject of a series of studies examining characteristics of consumption and digestive processing of food. Diet of young lemon sharks and many other sharks is dominated by teleosts. Feeding by lemon sharks is asynchronous, intermittent, and exhibits no pattern of periodicity. A meal is completely evacuated from the stomach of lemon sharks 25–41 hours after feeding, depending on meal type and temperature. Fecal production continues for 68–82 hours after feeding in the lemon shark. A relatively long period of time is also required for digestive processing of food in other species of sharks. Lemon sharks absorb energy from food with an efficiency similar to that of most teleosts. Daily ration has been estimated at 1.5–2.1% body weight/day, which is intermediate in comparison to estimates for other species of sharks and which is low in comparison to most teleosts. Lemon sharks are able to convert ingested energy to energy stored as growth as efficiently as many teleosts. Slow rates of digestion and consumption are factors which probably limit growth in the lemon shark and other elasmobranchs. Our findings for the lemon shark are compared with information gathered for other species of sharks.

Introduction

Sharks are one of the most abundant apex predators in the sea, playing a major role in the exchange of energy between upper trophic levels of the marine environment. Yet studies of consumption and feeding ecology of sharks are few, and knowledge of their role in the marine ecosystem is very limited. Although there are numerous lists of food items found in the stomachs of sharks (Baughman and Springer 1950; Clark and von Schmidt 1965; Randall 1967; Dahlberg and Heard 1969), there have been very few quantitative reports of various prey and fewer estimates of the amount of food consumed on an annual or daily basis. There are also few descriptions of feeding behavior or activity patterns associated with prey selectivity of predatory sharks. In addition there is little information on digestive

processes or the efficiency with which energy is absorbed and converted to growth.

The lemon shark (*Negaprion brevirostris*), which ranges from New Jersey to Brazil, is particularly abundant off Florida and in waters of the Bahamas (Springer 1950; Compagno 1984), and may represent an important energy sink in these areas of local abundance. To more fully define the role of the lemon shark in the tropical marine environment, we have been studying many factors, including diet, feeding habits, digestive physiology, growth, and other energetic parameters of this species. The following is a review of our observations about what, when, how much, how often and how efficiently lemon sharks eat; and what happens to food once it is ingested. These findings are then compared with information available for other species of sharks, and a synthesis is attempted.

Table 1.
Teleost prey in the stomachs of sharks.

Species	% occurrence of ^a teleosts in stomachs	Reference
<i>Prionace glauca</i>	90	Stevens 1973
<i>Carcharhinus leucas</i>	86	Tuma 1976
<i>C. leucas</i>	80	Snelson et al. 1984
<i>Triaenodon obesus</i>	78	Randall 1977
<i>P. glauca</i>	75	Tricas 1979
<i>Negaprion brevirostris</i>	71	Cortes and Gruber, In press
<i>Sphyrna lewini</i>	68	Clarke 1971
<i>Isurus oxyrinchus</i>	67	Stillwell and Kohler 1982
<i>Carcharhinus plumbeus</i>	37	Medved et al. 1985
% contribution of ^b teleosts in stomachs		
<i>N. brevirostris</i>	88	Schmidt 1986
<i>N. brevirostris</i>	74	Cortes 1987
<i>Squalus acanthias</i>	74	Bowman 1986
<i>Dalatias licha</i>	71	Matallanas 1982
<i>S. acanthias</i>	55	Jones and Geen 1977
<i>Triakis semifasciata</i>	50	Talent 1976
<i>Scyliorhinus canicula</i>	3-6	Lyle 1983

^aPercentage occurrence of teleosts = stomachs containing teleosts/stomachs sampled.

^bPercentage contribution of teleosts based on weight, volume, or index of relative importance.

Diet

The impact of sharks on a particular trophic level may be determined by knowing the amount and diversity of prey consumed. Sharks are abundant, wide ranging, and some compete with man by consuming commercially important species. Studies of the diets of sharks have been useful in evaluating the degree of predation on certain fish stocks and the level of competition with man. For example, fishermen accused the spiny dogfish, *Squalus acanthias*, of preying upon herring and young salmon to an extent that they represented a real competition to commercial and recreational fisheries (Ketchen 1975). However, until a quantitative study of the diet of these sharks was conducted (Jones and Geen 1977), there was little basis for refuting such claims.

The importance of teleosts in the diet of sharks is demonstrated by their prominence in the stomachs of many species of sharks (Table 1). Cortes and Gruber (In press) investigated the diet of the lemon shark by examining stomach contents of sharks caught with monofilament gill nets or set line off the Bahamas and Florida Keys. In three such studies, teleosts were the dominant prey items, accounting for 74% of stomach contents on the basis of relative importance. In a limited study, Schmidt (1986) noted that teleosts contributed 88% of the diet of lemon sharks caught in Florida Bay.

Nonteleosts (not including marine mammals or elasmobranchs) form about 10% of the diet of young lemon sharks, but appear to be more important in other species of sharks, and may even dominate the diet of some sharks (Table 2). For example, young leopard sharks, *Triakis semifasciata*, and lesser spotted dogfish, *Scyliorhinus canicula*, feed almost exclusively on nonteleost prey, and young sandbar sharks, *Carcharhinus plumbeus*, also feed primarily on crustaceans (Talent 1976; Lyle 1983; Medved et al. 1985).

Marine mammal flesh was not found in the stomachs of lemon sharks, but occurs in the stomachs of other sharks. A few sharks, such as the cookie cutter, *Isistius brasiliensis*; the tiger, *Galeocerdo cuvier*; and the great white, *Carcharodon carcharias*, may be especially adept at feeding upon marine mammals (Jones 1971; Taylor and Naftel 1978; Corkeron et al. 1987). However, the presence of marine mammal flesh in stomachs of other sharks such as the bull, *Carcharhinus leucas*; the Greenland, *Somniosus microcephalus*; the blue, *Prionace glauca*; the mako, *Isurus oxyrinchus*; the six-gill, *Hexanchus griseus*; and the dusky, *Carcharhinus obscurus*, is much less frequent, and may be a result of opportunistic feeding upon dead or dying animals (Bell and Nichols 1921; Templeman 1963; Stevens 1973; Stillwell and Kohler 1982; Ebert 1986; Gruber, pers obs).

Cortes (1987) found that elasmobranchs formed approximately 7% of the diet of larger lemon sharks. Elasmobranchs are especially important in the diet of several

Table 2.

Nonteleost prey in the stomachs of sharks. M = mollusks, CR = crustaceans, R = reptiles, I = variety of invertebrates, and P = polychaetes.

Species	% occurrence of ^a nonteleosts in stomachs	Reference
<i>Prionace glauca</i>	76 M	Tricas 1979
<i>Carcharhinus plumbeus</i>	73 M, CR	Medved et al. 1985
<i>Sphyrna lewini</i>	73 CR	Clarke 1971
<i>Triacodon obesus</i>	26 M	Randall 1977
<i>P. glauca</i>	25 M	Stevens 1973
<i>Carcharhinus leucas</i>	15 CR, R	Tuma 1976
<i>Isurus oxyrinchus</i>	15 M	Stillwell and Kohler 1982
<i>C. leucas</i>	6 CR	Snelson et al. 1984
% contribution of ^b nonteleosts in stomachs		
<i>Triakis semifasciata</i> (adult)	99 I	Talent 1976
<i>Scyliorhinus canicula</i>	94-97 CR, M, P	Lyle 1983
<i>T. semifasciata</i> (juvenile)	50 I	Talent 1976
<i>Squalus acanthias</i>	40 CR, M	Jones and Geen 1977
<i>S. acanthias</i>	26 CR, M, P	Bowman 1986
<i>Dalatias licha</i>	12 CR	Matallanas 1982
<i>Negaprion brevirostris</i>	12 CR	Schmidt 1986
<i>N. brevirostris</i>	10 CR, M	Cortes 1987

^aPercentage occurrence = stomachs containing nonteleosts/stomachs sampled.

^bPercentage contribution = based on weight, volume, or index of relative importance.

other species of shark, such as the hammerhead, *Sphyrna mokarran*; the bull; the Galapagos, *Carcharhinus galapagensis*; and the tiger shark (Springer 1960; Lineaweaver and Backus 1969; Randall 1977). Other sharks, including the soupfin, *Galeorhinus galeus*; the sandbar; the blue; the kitefin, *Dalatias licha*; the mako; and the sixgill, occasionally feed upon sharks and rays (Olsen 1954; Springer 1960; Stevens 1973; Tricas 1979; Matallanas 1982; Stillwell and Kohler 1982; Ebert 1986).

Hobson (1963) suggested that sharks refrain from feeding on members of their own species, and Tuma (1976) noted that Nicaraguan shark fishermen were reluctant to use shark for bait, because of its relatively low catch rate compared to other bait. Yet Vorenberg (1962) reported that cannibalism could be induced when lemon and bull sharks were excited by the presence of bait. Under natural conditions the lemon shark is cannibalistic. The authors have found small lemon sharks in the stomachs of larger lemon sharks at several locations off the Bahamas and Florida Keys. Budker (1971) states that the cannibalistic tendencies of hammerhead sharks have long been known, and Snelson et al. (1984) described cannibalism in the bull shark.

Springer (1960) concluded that pregnant sharks cease feeding when they enter nursery areas, as a protection measure for the young. Olsen (1984) reached the same conclusion. However, full term pregnant sharks are commonly captured with baited hooks (Clark and von Schmidt 1965;

Tuma 1976), and we have regularly observed hooked female lemon sharks giving birth while on the longline in nursery areas at Bimini, Bahamas (Gruber 1988). The preferred bait of these full term females appears to be small sharpnose sharks, *Rhizoprionodon porosus*. Such observations cast doubt upon the theory that pregnant female sharks cease feeding upon entering nurseries for parturition.

A large amount of indigestible material is found in the stomachs of sharks. Plant material accounted for 11% of stomach contents of the lemon shark (Cortes and Gruber, In press). In addition, Schmidt (1986) found plant material in 11% of lemon shark stomachs that he examined. A similar percentage of stomach contents consisted of plant material, mud and stones in the spiny dogfish (Jones and Geen 1977). Plants, stones and other indigestible bottom material have been found in the stomachs of angel, *Squatina* sp.; Port Jackson, *Heterodontus portusjacksoni*; blue; leopard; and mako sharks (Lineaweaver and Backus 1969; McLaughlin and O'Gower 1971; Stevens 1973; Talent 1976; Stillwell and Kohler 1982). Although this plant matter may be of nutritive value, we believe that it is the result of the benthic feeding habits of the sharks.

There are many stories of metallic and indigestible objects recovered from the stomachs of sharks (Lineaweaver and Backus 1969; Budker 1971), or in which sharks have become entrapped (Herz 1940; Bird 1978). Whether these objects are accidentally ingested with prey, or by a shark investigating potential prey, the indiscriminate feeding

habits of some sharks is apparent. Moss (1984) suggested that sharks may consume metal objects because they are attracted by their electric field. Tiger sharks are especially renowned for the wide variety of indigestible material found in their stomachs (Lineaweaver and Backus 1969). Baldridge (1982) proposed that tiger sharks ingest indigestible items such as stones or shells as a means of buoyancy control.

Thus, quantitative reports of stomach contents suggest that the diet of most sharks is dominated by teleosts, but nonteleost prey are consumed to a considerable extent by some species. Marine mammals are important in the diet of only a few species of sharks, while elasmobranchs are common in the diet of others, including pregnant females, and cannibalism certainly occurs. Indigestible bottom material is consumed along with prey, and a wide range of indigestible items are found in the stomachs of a few species of sharks.

Feeding Habits

Opportunistic Versus Selective Feeding

We consider an opportunistic feeder as one that generally consumes whatever prey is encountered, rather than one that is selective and ignores available prey for a preferred type. We would expect stomachs of opportunistic feeders to contain a variety of prey, similar in composition and abundance to the prey fauna in the predator's habitat. Stomachs of selective feeders would be expected to contain a predominant prey-type, which in some cases might be less abundant than other prey items in the habitat. However, if a predator were selectively feeding on the most abundant prey, the difference between opportunism and selectivity might be difficult to detect.

Sharks are often considered to eat whatever they happen to encounter. Budker (1971) stated that for a shark to avoid death by starvation it must be in a constant state of readiness, living a life of perpetual ambush, pursuit, and attack, always actively engaged in the search for food. He considered sharks to be such opportunistic feeders that their stomach contents were a good indication of the abundance of marine fauna in a given area. According to Springer (1960), most sharks are opportunistic feeders out of necessity, existing on a feast or famine regimen owing to their ineptness at catching prey. Springer (1967) found no indication that the kind of internal drive that man knows as hunger operates or even exists for sharks. Such reports reflect the opinion held by many, but much more information has recently been gathered on feeding habits of sharks, providing evidence for a very different view. Some species of sharks indeed appear to be opportunistic, but the extent to which they are opportunistic or selective feeders is not well defined.

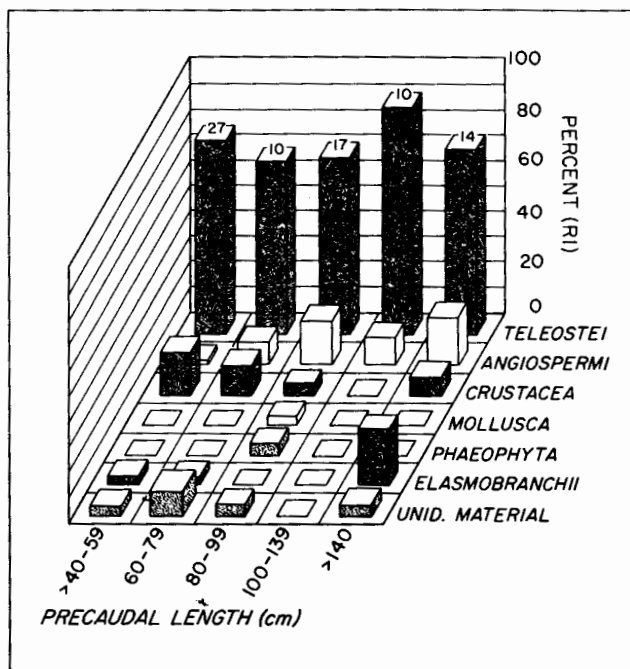


Figure 1.

Variation in the Relative Importance Index (RI) of the major food categories in the diet of five length-classes of lemon sharks off Bimini, Bahamas, and the Florida keys ($N = 78$). Sample size for each length class is given in the figure. (From Cortes and Gruber, In press.)

The opportunistic feeding nature of sharks is suggested by changes in diet with size, season, and habitat. Lemon sharks occupy shallow bays and lagoons during the first few years of life and appear to stray little from these habitats. As they grow, they move off the flats into deeper water, increasing home range, variety of habitats and prey encountered (Gruber 1982; Gruber 1984; Gruber et al. 1988). The diversity of the diet also increases and elasmobranchs, adult jacks, and lobster become increasingly important (Fig. 1). Springer (1960) also noted movement out of nurseries and subsequent changes in the diet of lemon sharks as they increased in size.

Ontogenetic change in diet with increasing size is common in other species of sharks, as is the use of relatively protected environments as nursery areas. The diet of the young leopard shark consists almost exclusively of crabs; older leopard sharks are not restricted to nursery areas and have a much more varied diet, nearly half of which is fish (Talent 1976). Springer (1960) noted that mature sandbar sharks feed on a wide variety of fish, crustaceans, and octopus, while Medved et al. (1985) found that blue crabs and menhaden comprised the majority of the diet of young sandbar sharks caught in an estuary. Juvenile Port Jackson sharks occupying bays and estuaries feed on soft bodied invertebrates, while the main prey of adults is a variety of echinoderms, mollusks, and crustaceans (McLaughlin

and O'Gower 1971). Young soupfin sharks, which inhabit bays with subtidal flats, feed largely upon fish, crustaceans, and mollusks; but adults feed around rocky areas and consume more fish and octopus (Olsen 1954). As spiny dogfish grow, their diet becomes more diverse and shifts from invertebrates to fish (Jones and Geen 1977). Larger kitefin sharks consume more crustaceans, teleosts, and elasmobranchs, while the importance of cephalopods in the diet declines with an increase in size (Matallanas 1982). Lyle (1983) found that young lesser spotted dogfish ate more crustaceans, while larger specimens ate more mollusks and fewer crustaceans. Finally, when mako sharks had attained a size greater than 150 kg, they were able to feed on very large prey such as swordfish (Stillwell and Kohler 1982).

These ontogenetic changes in diet indicate that in some species of sharks, juveniles have a restricted diet associated with a particular habitat such as a nursery ground. In these areas young sharks may be less susceptible to predation, but also may encounter fewer potential prey. Particularly abundant prey, or one which is easily caught, may dominate diets of young sharks which live in nursery areas.

Seasonal shifts in the diet of young lemon sharks have not yet been confirmed, but it appears that there may be a peak in consumption of toadfish, *Opsanus beta*, which coincides with increased vocalization during toadfish mating season each April (Cortes 1987). There have been many reports of seasonal changes in the diet of other sharks. As seasonal abundance of different species of squid fluctuates, the amount of each species consumed by blue sharks also fluctuates (Tricas 1979). Talent (1976) found that leopard sharks ate primarily fish during the summer, but primarily crabs and clams during the fall. The importance of bluefish and squid in the diet of the mako shark shifts with season (Stillwell and Kohler 1982). Bluefish are more important during the spring and winter, but migrate inshore during the summer, and are replaced in importance by cephalopods. Matallanas (1982) discovered that while teleosts were the most important prey item in the diet of kitefin sharks throughout the year, the items of secondary importance shifted with season. Sharks were the second most common item in spring and winter, crustaceans in summer, and cephalopods in the fall. When herring were concentrated in large numbers during spawning periods, they became a major prey item in the diet of the lesser spotted dogfish (Lyle 1983). During seasonal migrations, certain fish may become important dietary items for the soupfin shark (Olsen 1954).

Habitat may have a significant influence in the type of prey recovered from the stomachs of sharks. Cortes (1987) found little difference between the diet of lemon sharks sampled off the Florida Keys and Bimini, Bahamas. However, Schmidt (1986) recorded large numbers of shrimp in the stomachs of lemon sharks caught in Florida Bay, while few shrimp were found in stomachs examined by Cortes.

The contribution of fish and crustaceans to the diet of scalloped hammerhead sharks, *Sphyrna lewini*, varied from one location to another in Kaneohe Bay, Hawaii (Clarke 1971). The relative importance of mollusks and demersal fish in the diet of lesser spotted dogfish also varied with sampling location (Lyle 1983). Olsen (1954) noted that the diet of young soupfin sharks was dependent on which estuary the sharks inhabited. Bowman (1986) found that spiny dogfish ate more squid in deep water, but switched to fish in shallow water. The percentage occurrence of prey items in stomachs of mako sharks has also been correlated with location (Stillwell and Kohler 1982). Clarke and Stevens (1974) found different cephalopod species in the stomachs of blue sharks captured at two different locations. Further opportunism is suggested by their feeding on fish in the epipelagic zone, squid in deep water, and crustaceans and gastropods when feeding on the bottom (Stevens 1973). The diet of blue sharks also varies depending on the availability of anchovies, squid, or salmon (Le Brasseur 1964; Tricas 1979). Horn sharks, *Heterodontus francisci*, were reported to abandon nocturnal feeding habits and to feed during the day when large numbers of dead or dying fish were present (Finstad and Nelson 1975). These findings demonstrate that sharks can switch to different prey in different habitats and that food habits in one location may not be representative of food habits of the same species elsewhere. Thus, limited sampling of stomach contents of sharks, both in time and space, must be interpreted with caution.

Tiger and bull sharks provide examples of species which have broad feeding habits. The tiger shark is considered to be an opportunistic feeder, preying on a wide range of organisms (Bell and Nichols 1921; Springer 1960; DeCrosta et al. 1984). Bull sharks select a wide variety of habitats, ranging from freshwater lakes and rivers, to coral reefs and flats throughout the tropical and subtropical oceans (Compagno 1984). Just as habitats selected by the bull shark are extremely diverse, so is the diet. Tuma (1976) found echinoderms, mollusks, crustaceans, mammals, teleosts, elasmobranchs, reptiles, and other items in the stomachs of bull sharks. These sharks were capable of capturing fast swimming fish, but consumed almost any type of animal matter available (dead or alive). Hobson (1963) believed that while sharks may feed on injured, distressed, or dead fish, they were capable of capturing highly motile, elusive prey. Versatile food habits are advantageous to the individual because feeding will not be limited to a particular prey item throughout the year. With sharks, this may allow for an increase in population density, a decrease in competition and a broadening of range and distribution (Talent 1976).

Shifts in prey selection may be due to changes in abundance, ease of capture of prey, or changes in density of shark populations (Talent 1976). It appears that in several species, the most abundant prey items in a habitat are also

the most heavily preyed upon. The most prominent prey items in the diet of juvenile lemon sharks appear to be among the most abundant organisms in the shallow water environments inhabited by the sharks; however, further studies directed toward this question are currently underway (Gruber, unpubl. data). Lyle (1983) concluded that the most common prey in the diet of lesser spotted dogfish were also the most abundant species in a survey of bottom fauna. A similar conclusion was reached by Clarke (1971) for the scalloped hammerhead shark and by Talent (1976) for the leopard shark.

Some shark species demonstrate the ability to select prey. Springer (1960) described the sandbar shark as a discriminating bottom feeder, which showed a preference for specific prey. Stillwell and Kohler (1982) suggested that the mako shark may selectively feed on larger bluefish to maximize rate of energy intake. Tricas (1979) observed several patterns of predatory behavior by blue sharks when they fed upon schools of spawning squid. The feeding patterns reported by Tricas varied with size and activity of shark, as well as the physical configuration and alertness of squid. Even the bull shark has shown evidence of selective feeding, passing up abundant species of fish which were regularly consumed by other species of shark (Snelson et al. 1984).

The observation of a preference for specific prey, as well as changes in prey selectivity, introduce the question concerning the degree to which sharks are selective in their feeding habits. The relationship between opportunistic and selective feeding in sharks is not evident to us. Both opportunistic and selective feeding habits can be described for sharks, and even for individuals of the same species. Many sharks may fit the description of opportunistically-selective feeders. When food is abundant, they may select a specific item, which may maximize energy intake with a minimum of energy expenditure. When food is less plentiful, they may not be afforded the luxury of choice, and may feed on almost any prey which is available. In lemon sharks, the interval between meals is relatively long (Cortes 1987). Sharks that eat infrequently may feed when a preferred food item is encountered, rather than consuming less desirable prey more frequently.

Optimal Foraging

The theory of optimal foraging is based on the evolutionary premise that individuals within a population that forage most efficiently and that maximize their net rate of energy intake will possess greater fitness and contribute their genes to future generations (Townsend and Winfield 1985). There are two extremes in feeding habits that maximize foraging efficiency: indiscriminate feeding at low prey abundance, and selective feeding on larger, energy rich items when prey is abundant (Knights 1985). Changes in sensory ability that occur with age may strongly influence feeding strategy. Young fish, growing at a maximum rate,

have a large appetite and are generally less selective of prey. They may also lack the sensory capability to distinguish between potential prey items. As visual and chemical cues are learned, older fish may become more selective of larger, higher quality prey (Knights 1985).

There is considerable confusion and disagreement about the usefulness of this theory, but it is possible to briefly view the feeding habits of the lemon shark from this perspective. First we can examine changes in sensory capability of lemon sharks as they age. Although the lemon shark is farsighted, young lemon sharks appear to have better visual acuity than older sharks (Hueter and Gruber 1982). Beulig (1982) found that young lemon sharks did not instinctively recognize the sound of prey, but had to learn specific sounds associated with the availability of food. Thus, as their senses develop and prey abundance increases, young lemon sharks should feed on a more narrow range of prey, increasing their selectivity as they grow. However, Cortes (1987) found that the diet of lemon sharks become more diverse with age. So young lemon sharks may lack the ability to catch a variety of prey or may simply not encounter that variety of prey in the nursery habitat. Similar limitations may apply to other species of shark that inhabit areas of low productivity at early ages. In these cases sharks may not appear to conform to the tenets advanced in the theory of optimal foraging. Casey et al. (1985) suggested that sandbar sharks may reach a size where food, oxygen, or a combination of several factors become limiting and this is the putative mechanism which triggers juveniles to leave nursery areas for offshore waters. As more information is gathered about the life-history strategies of elasmobranchs and about optimal foraging in other taxa, many of the existing principles may be more readily understood.

Finally, there are several reports of sharks feeding cooperatively. Although the lemon shark may congregate loosely in schools (Gruber et al. 1988), there has been no documentation of cooperative hunting in this species. Lineaweaver and Backus (1969) state that the oceanic whitetip shark, *Carcharhinus longimanus*, may hunt cooperatively and Budker (1971) made a similar statement about thresher, *Alopias* sp., and sandtiger sharks, *Eugomphodus taurus*. Randall (1977, 1986) commented on the possibility of cooperative hunting by other species of sharks. Talbot (F.H. Talbot, Director, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118, pers. comm., June 1987) and others have observed blacktip reef sharks, *Carcharhinus melanopterus*, hunting in groups and chasing small teleosts out of the water onto the shore. The blacktips then beached themselves and fed upon the stranded fish.

Feeding Patterns

It is not only important to know what sharks eat, but also when and how often they eat. Knowledge of food habits

Table 3.
Percentage of sharks caught that had empty stomachs.

Species	% empty stomachs	Reference
Sharks caught using bait		
<i>Notorhynchus cepedianus</i>	92	Herald and Ripley 1951
<i>Carcharhinus amblyrhynchos</i>	80	McKibben and Nelson 1986
<i>Negaprion brevirostris</i>	80	Gruber 1984
<i>Carcharhinus leucas</i>	58	Tuma 1976
<i>Carcharhinus plumbeus</i>	55	Wass 1973
<i>Carcharhinus galapagensis</i>	54	De Crosta et al. 1984
<i>C. amblyrhynchos</i>	48	De Crosta et al. 1984
<i>Isurus oxyrinchus</i>	40	Stillwell and Kohler 1982
<i>Prionace glauca</i>	39	Stevens 1973
<i>P. glauca</i>	37	Clarke and Stevens 1974
<i>Galeorhinus galeus</i>	26	Olsen 1954
<i>Galeocerdo cuvier</i>	20	De Crosta et al. 1984
<i>P. glauca</i>	6	Tricas 1979
Sharks caught using net or other nonbait methods of capture		
<i>Squalus acanthias</i>	74	Bowman 1986
<i>Triacodon obesus</i>	59	Randall 1977
<i>S. acanthias</i>	36	Jones and Geen 1977
<i>N. brevirostris</i>	26	Cortes and Gruber In press
<i>Dalatias licha</i>	17	Matallanas 1982
<i>P. glauca</i>	17	Le Brasseur 1964
<i>Triakis semifasciata</i>	16	Talent 1976
<i>C. plumbeus</i>	13	Medved et al. 1985
<i>Scyliorhinus canicula</i>	1	Lyle 1983

is vital in assessing the ecological requirements of a species (Talent 1976), and information gathered on diet and feeding habits adds insight into the biology and distribution of a species (Stillwell and Kohler 1982). Two questions of fundamental importance to understanding the interaction between a predator and food resources are "How often and how much does the predator consume?" (Hall 1987).

The feeding schedule of the lemon shark appears to be characterized by short bouts, followed by longer periods of digestion, with little or no feeding in the interim. This pattern appears to hold for other species as well. For example, individuals are often caught and found to have empty stomachs. Cortes (1987) found that 26% of lemon sharks captured with gill nets had empty stomachs. This is low in comparison to values reported for other species (Table 3). Springer (1960) wrote that a very large proportion of sharks in commercial landings had empty stomachs. This means that a large number of animals caught with bait had gone a substantial period of time without eating. Yet some individuals caught with bait have full stomachs, which reinforces the common perception that sharks are "gluttons" (Budker 1971). Lineaweaver and Backus (1969) reported large catches of sharks with full stomachs, and on other occasions poor catches characterized by a high percentage with empty stomachs.

Many food items in the stomachs of sharks are well digested. In the lemon shark, 28% of stomachs contain-

ing food had a single item in a late stage of digestion (Cortes 1987). The same was true for 21.5% of sandbar sharks that had food in their stomachs (Medved et al. 1985). Thus, nearly 50% of lemon and sandbar sharks had little or no food in their stomachs when captured. Springer (1960) noted that stomach contents of sandbar sharks were usually not identifiable owing to an advanced state of digestion. A high frequency of unidentified prey in late stages of digestion is characteristic of the kitefin (Matallanas 1982) and soupfin sharks (Olsen 1954). Stevens (1973) was able to identify only 50% of prey in the stomachs of blue sharks, because most items were in an advanced state of digestion. It is apparent that the majority of sharks that were attracted to bait were those which had relatively empty stomachs or those which had recently eaten, but were still inclined to consume additional food. Thus, these sharks feed for short periods of time.

The number of food items in the stomachs of lemon sharks caught in nets was low. Nearly 80% of stomachs containing food had only one or two prey items (Cortes 1987). Medved et al. (1985) reported a similar finding for the sandbar shark, where 60% of stomachs with food contained a single item and 90% had three items or less. Most blue shark and spiny dogfish stomachs also contained only one or two food items (Stevens 1973; Jones and Geen 1977). Tricas (1979) found a low average number of prey in the stomachs of blue sharks during most of the year.

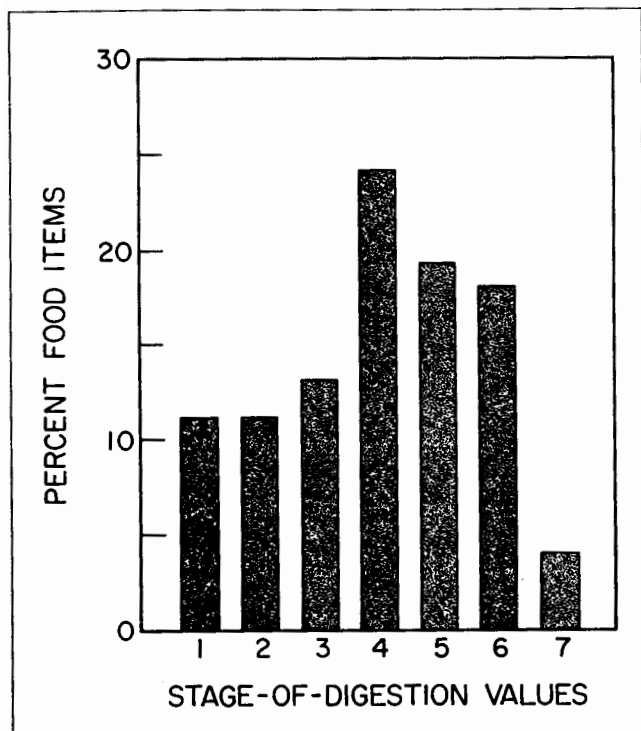


Figure 2.

Frequency distribution of stage-of-digestion values assigned to food items ($N = 110$) consumed by young lemon sharks captured off the Florida keys. (From Cortes 1987.)

The average number of food items in the stomachs of lesser spotted dogfish was between four and six (Lyle 1983). In each of these studies, multiple food items were usually in a similar stage of digestion. Cortes (1987) and Medved et al. (1985) assigned stage-of-digestion values, based on rates of digestion in control studies, to food items found in stomachs of lemon and sandbar sharks respectively. Examination of the values for multiple food items allowed them to calculate feeding duration for these two species. Feeding duration of the lemon shark was estimated as 10–11 hours and at 7–9 hours for the sandbar shark. Feeding frequency of the lemon shark was estimated as 32 hours. Thus, an average lemon shark would actively feed for 10–11 hours and then fast for the next 32 hours. Theoretically, if these sharks had been feeding continuously, multiple food items at various stages of digestion would be found in their stomachs. Yet the opposite trend was observed.

Our findings indicate that frequency of feeding in the lemon shark is dependent on factors which commonly influence rate of consumption in other aquatic vertebrates, such as rate of digestion and energy content of food, rather than their ability, or inability to capture prey. After a lemon shark has consumed a meal or successive meals, feeding appears to be reduced. Sharks very likely encounter prey during this time, but they may not be attracted to a poten-

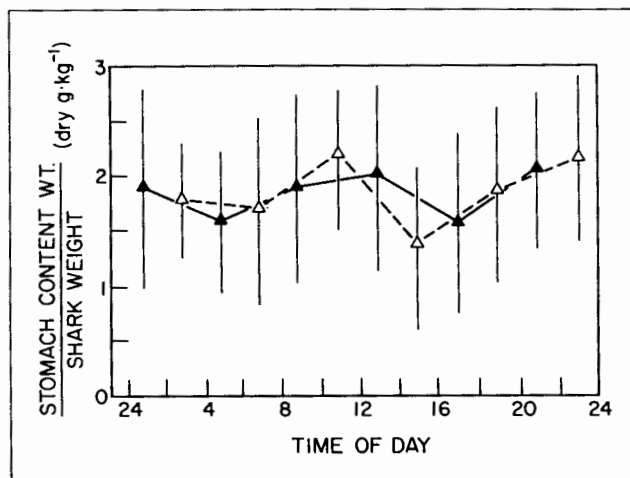


Figure 3.

Diel variation in mean ratio of dry weight of stomach contents to wet weight of shark (g/kg). Solid triangles are the means at the mid-point of each 4 h time interval, starting at 2300 hours; open triangles are the means at the mid-point of each 4 h time interval, starting at 0100 hours. Vertical lines designate ± 1 SD. (From Cortes 1987.)

tial meal because their stomachs are relatively full. When the stomach is nearly empty, feeding activity increases, and prey may once again be actively sought.

Finally, a cyclical feeding pattern has been described for the captive lemon shark. Peak consumption is followed by a few days of reduced consumption, when appetite is re-established (Graeber 1974; Longval et al. 1982). Casey et al. (1985) noted a similar pattern for captive sandbar sharks. All of these observations point to a short period of active feeding, followed by a longer period of digestion with reduced feeding activity. There is little evidence to support the supposition that sharks feed continuously, and abundant evidence that feeding motivation waxes and wanes as in most other vertebrates.

Cortes (1987) found food in all stages of digestion in the stomachs of lemon sharks sampled at hourly intervals (Fig. 2). This suggested that lemon sharks feed asynchronously, i.e., there is no particular time of day or night when a greater number of sharks are feeding. Data from Medved et al. (1985) and Matallanas (1982) supported these findings for other shark species.

There is a widespread belief that sharks are more active at night and feeding activity increases during this time (McKenzie and Tibbo 1964). Both laboratory (Nelson and Johnson 1970; Casterlin and Reynolds 1979; Nixon and Gruber 1988) and field studies (McLaughlin and O'Gower 1971; Finstad and Nelson 1975) have shown that metabolic rate or activity of some sharks, including the lemon shark, increases at night. Yet Cortes (1987) found no temporal difference in the amount of food in stomachs of lemon

sharks (Fig. 3). Medved et al. (1985) also found no significant day-night differences in stomach contents of sandbar sharks. Actual increase in feeding activity by the lemon and sandbar sharks may be masked by crepuscular feeding habits, or by occasional opportunistic feeding throughout the day or night. Olsen (1954) reported that tides may be a factor in the feeding activity of soupfin sharks, but tidal cycle did not influence feeding of sandbar or lemon sharks (Medved et al. 1985; Cortes 1987). It appears then, for at least the lemon and sandbar sharks, and presumably others, feeding is intermittent, asynchronous, and does not exhibit measurable patterns of periodicity.

Digestion

The digestive abilities of sharks are confusing and difficult to characterize. Sharks may cease feeding for long periods of time for no apparent reason, presumably relying on energy stores in the liver during weeks and even months of starvation (Lineaweaver and Backus 1969; Budker 1971; D.R. Nelson, Department of Biology, California State University, Long Beach, CA 90840, pers. comm., June 1987). Springer (1960) felt that larger prey species were frequently of a less digestible type, and were taken by sharks in desperation when no other food was available. He also hypothesized that the digestive processes of sharks were inhibited when they swallowed large quantities of decomposing flesh of sharks and rays. The acidity of a stomach would decrease due to

... the continuous liberation of ammonia through the action of enzymes produced during the course of ordinary putractive decomposition of the urea that normally occurs in sharks.

Springer (1960) reported that stomachs of sharks which contained large amounts of decomposing shark flesh had a pH above 8.0, whereas those containing fish, turtles, birds, or small amounts of shark flesh had a pH of 4.0 or below.

Budker (1971) reported that the stomach of a shark may retain food in a undigested state for long periods of time. He describes an account of two dolphin fish, *Coryphaena hippurus*, in a perfect state of preservation being recovered from the stomach of a tiger shark that was held in captivity for a month. The shark appeared to have preserved the dolphin, while ingesting and regurgitating horsemeat. This was presumably accomplished by restriction of digestive secretions, compartmentalization, or secretion of preservative substances. Budker (1971) also reported that human flesh had remained undigested in the stomach of a tiger shark for days and even weeks.

The means by which sharks achieve these unusual feats is not clear. Digestive enzymes which are produced in the

alimentary tracts of elasmobranchs are substances common to teleosts and other vertebrates (Fänge and Grove 1979). Dobreff (in Barrington 1957) found that HCl production continued in the stomach of elasmobranchs deprived of food for 112 days. Acidity declined with the absence of food, but HCl was still secreted in detectable quantities until the animal died of starvation. Observation of feeding behavior in captive sharks, such as prolonged unwillingness to feed, or preservation of food, does not necessarily represent natural feeding or digestive characteristics. Stress associated with captivity can lead to refusal of food and unusual feeding behavior (Van de Elst et al. 1983). Studies of the digestive physiology of elasmobranchs are needed to explain these unusual phenomena.

Most absorption of nutrients takes place in the intestine, and this is an early step in making useful energy available for growth or metabolism (Fänge and Grove 1979). The rate of the passage of food through the digestive tract can have important ramifications in the amount of nutrient absorbed across the gut wall. The longer a meal is in the digestive tract, the longer it is subject to the processes of enzymatic digestion and absorption, and the greater the amount of nutrient that can be absorbed (Windell 1978).

Total retention time of a meal has been measured in the lemon shark by an x-radiographic technique, where barium sulfate was incorporated into food (Wetherbee et al. 1987). A minimum of 68–82 hours was required for a meal to be entirely eliminated from the digestive tract of the lemon shark (Fig. 4). Budker (1971) reports that a period of 2–6 days is a typical residence time of a meal in the digestive tracts of sharks, and gives a value of 18 days as the time food remained in the digestive tract of dogfish. It is apparent that food passes through the alimentary tract of sharks at a relatively slow rate compared to most teleosts. For example, the average time for a meal to be completely emptied from the digestive tract of teleosts studied at 20–25°C is less than 50 hours (Lane and Jackson 1969; Fänge and Grove 1979).

Differences in digestive processes between elasmobranchs and teleosts are not limited to the rate at which food passes through the gastrointestinal tract. Most teleosts have a tubular intestine, while elasmobranchs have a spiral valve intestine, which increases surface area for absorption without taking up additional space in the body cavity (Budker 1971). This space conservation measure may be correlated with the large elasmobranch liver required for buoyancy, or with retention of developing embryos in utero (Moss 1984). The digestive and absorptive capabilities of elasmobranchs had not been studied prior to Wetherbee (1988). He found that the lemon shark is able to absorb energy from a meal with an efficiency comparable to that of most teleosts. Absorption efficiency of lemon sharks is not unusually high or low, despite their having a spiral valve intestine, a prolonged food retention time and an extended period of digestion.

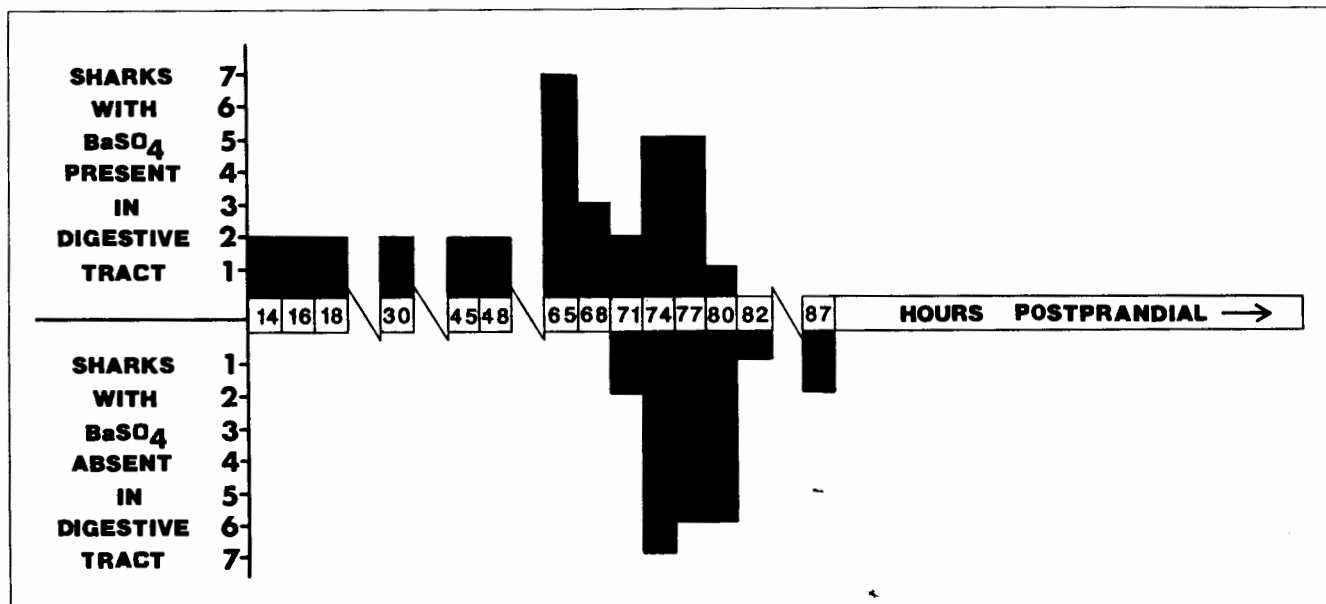


Figure 4.

Histogram showing the presence or absence of barium sulfate (BaSO_4) in the digestive tract of lemon sharks. The first observation in which BaSO_4 had been completely voided was at 71 hours, while the last occurrence of BaSO_4 was at 80 hours.

Consumption

The rate at which food energy passes through an individual, sets a limit on the rate of production for an individual or population (Hall 1987). Food consumed by sharks represents the sole energy source for growth and metabolism, and estimates of consumption can be valuable in assessing basic biological information, ecological relationships, the extent of predation and competition, environmental conditions for growth, impact on commercially important fish or other stocks, and rational exploitation of populations.

Two basic methods have been used to estimate consumption for fishes. One method uses laboratory experiments to derive parameters relating to growth, metabolism, excretion and digestion. The second method estimates consumption based on the amount of food found in stomachs sampled in the wild, in conjunction with measurement of the rate of gastric evacuation (Windell 1978). Both methods rely on experiments with captive animals, and for this reason, there have been very few estimates of consumption for elasmobranchs. The difficulty of keeping and sampling sharks in captivity has limited laboratory studies of many aspects of elasmobranch biology (Gruber and Myrberg 1977; Martini 1978; Gruber and Keyes 1981). Consumption cannot be estimated by using description of prey items, weight, or volume alone. This is because the amount of food found in a stomach is a function of the rate of gastric evacuation, amount of food initially consumed, and time (Windell 1978).

Gastric Evacuation

Two estimates of the time required for complete evacuation of food from the stomachs of lemon sharks have been derived. Schurdak and Gruber (1988) found that filets of blue runner, *Caranx chrysos*, were completely evacuated in approximately 24 hours, and the pattern of gastric emptying was exponential. Cortes (1987) found that a larger meal of a natural prey item was completely eliminated from stomachs in 28–41 hours, and was best described by a linear model. The difference in these two studies may be due to the use of smaller more friable food by Schurdak and Gruber, as well as temperature fluctuation in Cortes' study. Jobling (1986) reviews the influence of these factors on gastric evacuation and the mathematical models that are used to describe the rate of gastric evacuation in fish. He concludes that smaller more easily digested food is rapidly eliminated from stomachs in an exponential manner, while larger items are evacuated in a linear manner.

Medved (1985) showed that time required for complete gastric evacuation in the sandbar shark was 71–92 hours, much longer than that of the lemon shark (Table 4). The difference in time is greater than what might be expected based on their similar distribution, life history, and close phylogenetic relationship. It is likely that methodological differences exaggerated actual differences in gastric evacuation. Medved (1985) force fed sandbar sharks and used a stomach lavage technique to remove stomach contents. Force-feeding in teleosts has been shown to depress the rate of gastric evacuation and increase variation between

Table 4.
Estimates of time required for a meal to be completely evacuated from the stomachs of sharks.

Species	Hours for complete gastric evacuation	Temperature °C	Reference
<i>Squalus acanthias</i>	124	10	Jones and Geen 1977
<i>Carcharhinus plumbeus</i>	71-92	25	Medved 1985
<i>C. plumbeus</i>	48 +	—	Wass 1973
<i>Isurus oxyrinchus</i>	36-48	—	Stillwell and Kohler 1982
<i>Negaprion brevirostris</i>	28-41	20-29	Cortes 1987
<i>N. brevirostris</i>	24	25	Schurdak and Gruber 1988
<i>Prionace glauca</i>	24 +	—	Tricas 1979

individuals (Windell 1966; Swenson and Smith 1973). In the Medved study, stomachs were lavaged prior to a feeding trial; this treatment may have washed digestive enzymes from stomachs, delaying the onset of digestion and perhaps prolonging gastric emptying time. Cortes (1987) estimated time for complete evacuation of lemon shark stomachs by extrapolation from a gastric evacuation curve (Fig. 5). However, MacDonald et al. (1982) found that rate of gastric evacuation may peak after a time, so that a linear representation of evacuation rate, similar to Cortes' may be improper. Lemon sharks were also held at a slightly higher temperature than sandbar sharks. Temperature has been shown to hasten gastric emptying in teleosts (Jobling 1986). Considering the different techniques used by Medved and Cortes, it is likely that the actual times required for complete gastric emptying in the lemon and sandbar sharks are more similar than would appear from the results.

Other estimates of gastric evacuation rates for sharks are not well documented or are incomplete. Jones and Geen (1977) force fed spiny dogfish extremely high rations and estimated time for complete gastric emptying by fitting a straight line to the data and extrapolating to zero food. Stillwell and Kohler (1982) estimated time for complete gastric emptying for the mako shark based on examination of stomach contents and use of information from other species of sharks. Rate of gastric evacuation and time required for complete emptying were not actually measured in either of these studies. Wass (1973) found that sandbar sharks had food in their stomachs 48 hours after consumption of a meal but did not determine time for complete gastric evacuation. Tricas (1979) reported the presence of undigested food in stomachs of blue sharks 24 hours after consumption of a meal. Based on the few actual measurements and partial measurements of gastric evacuation, it is apparent that a substantially longer period of time is required for food to be completely eliminated from the stomachs of sharks than the stomachs of teleosts. Although gastric evacuation of several teleosts may require over 30 hours, the average time for complete gastric evacuation of

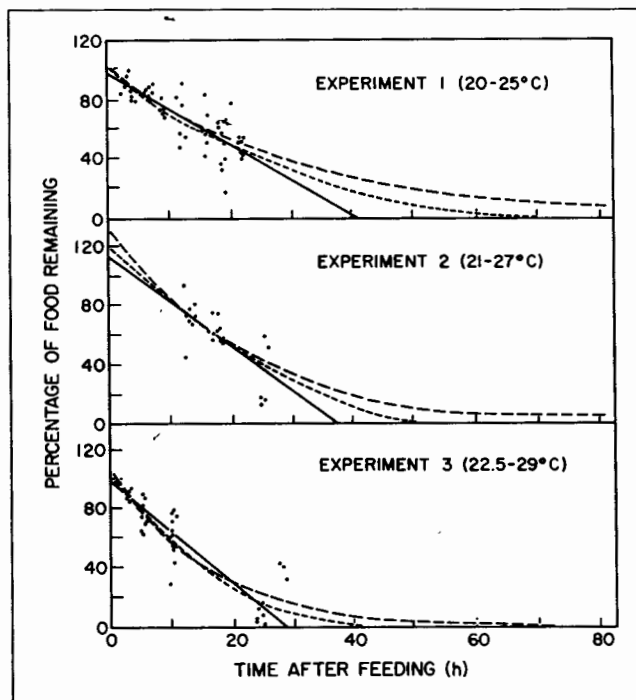


Figure 5.

Mathematical models fitted to gastric evacuation data of young lemon sharks fed snapper or white grunt, at three temperature regimes: linear (—), exponential (---), and square root (....). Percentage of food remaining in stomachs is expressed as dry weight. (From Cortes 1987.)

a meal measured for teleosts at a temperature close to 25°C is about 12 hours (Fänge and Grove 1979).

Daily Ration

Although an individual may not consume the same amount of food each day, or may not even feed daily, consumption expressed on a daily basis (daily ration) provides a useful means of comparison of ingestion rates for different

Table 5.
Estimates of daily ration for sharks.

Species	Daily ration % body weight/day	Reference
<i>Isurus oxyrinchus</i>	3.2	Stillwell and Kohler 1982
<i>Negaprion brevirostris</i>	1.5-2.1	Cortes 1987
<i>Squalus acanthias</i>	1.3	Jones and Geen 1977
<i>Carcharhinus plumbeus</i>	1.1	Medved et al. 1988
<i>N. brevirostris</i>	0.4-2.0	Clark 1963
<i>S. acanthias</i>	0.4	Brett and Blackburn 1978

Table 6.
Estimates of annual consumption for sharks.

Species	Daily ration % bw/d	Average body weight (kg)	Annual consumption (kg)	Body weight ^a consumed	Reference
<i>Isurus oxyrinchus</i>	3.1	69.0	781	11.3	Stillwell and Kohler 1982
<i>Negaprion brevirostris</i>	1.5-2.1	1.891	10.3-13.8	5.8-7.3	Cortes 1987
<i>N. brevirostris</i>	—	1.000	5.3-6.5	5.3-6.5	Bushnell et al. submitted
<i>Squalus acanthias</i>	1.3	0.107	0.51	4.7	Jones and Geen 1977
<i>Carcharhinus plumbeus</i>	1.1	1.882	7.6	4.0	Medved et al. 1988
<i>S. acanthias</i>	0.4	0.107	0.16	1.5	Brett and Blackburn 1978

^aBody weight consumed = number of times an equivalent of body weight is consumed in a year.

organisms. Daily ration of the lemon shark has been estimated at about 2% body weight per day (bw/d) (Cortes and Gruber, In press). Clark (1963) stated that lemon sharks held in captivity consumed between 0.4 and 2% bw/d and assumed that daily ration in the field was higher than in captivity because of the need for additional energy to capture prey. Gruber and Stout (1983) showed that captive lemon sharks kept under optimal conditions grew ten times faster than in the wild. The majority of additional growth observed by Gruber and Stout can be attributed to food intake levels, which were about 3% bw/d and well above those of wild lemon sharks. Changes in metabolic rate and stress would also influence growth rate in captivity sharks.

Table 5 lists estimates of daily ration for other species of sharks. Medved et al. (1988) obtained a value of 1.1% bw/d for daily ration of sandbar sharks. The lemon shark appears to consume almost twice as much food as the sandbar shark, but differing estimates of gastric evacuation rate may be partly responsible for different estimates of consumption. Another factor may be that lemon sharks grow more rapidly and to a greater size than sandbar sharks (Casey et al. 1985; Henningsen and Gruber, in prep.). If lemon sharks have a higher metabolic rate than sandbar sharks, they would require an increased level of intake for metabolism, yet reports of activity of these two species are somewhat conflicting (Medved and Marshall 1983; Nixon and Gruber 1988).

Daily ration of the spiny dogfish has been calculated to be 1.3% bw/d (Jones and Geen 1977) and 0.4% bw/d (Brett and Blackburn 1978), the difference attributable to methodology. Bowman (1986) cautioned that spiny dogfish caught at depth frequently regurgitate stomach contents when they are brought to the surface. This would result in a bias in determination of daily ration and the type of prey consumed; and the predatory impact that spiny dogfish have on fish populations would be underestimated.

Stillwell and Kohler (1982) estimated daily ration of the mako shark at 3.1% bw/d. Although this estimate was not based on measurement of the rate of gastric evacuation, a high level of consumption relative to other shark species might be expected. Mako sharks are fast swimming, highly active sharks, capable of maintaining a body temperature several degrees above that of ambient water (Carey and Teal 1969). Digestion rate, rate of food passage, and consequent ingestion rate may all be increased at higher ambient temperatures (Jobling and Davies 1979; Kaushik 1986). This may be especially true considering that the spiral valve is the warmest visceral organ in the mako shark (Carey et al. 1981). Mako sharks grow at a fairly rapid rate in comparison to many sharks (Pratt and Casey 1983). This also implies a high level of intake, assuming that assimilation and growth efficiencies are similar to those of cold bodied sharks.

Table 7.
Estimates of annual growth in mass for individual sharks of the species listed.

Species	Initial weight (kg)	Final weight (kg)	Weight gain (kg)	% body gain	Reference
<i>Negaprion brevirostris</i>	1.118	2.664	1.546	138	Henningsen and Gruber, in prep.
<i>Carcharhinus plumbeus</i>	1.349	2.415	1.066	79	Medved et al. 1988
<i>Squalus acanthias</i>	0.092	0.122	0.031	33	Jones and Geen 1977

Table 8.
 K values = slope of von Bertalanffy growth curve fitted to growth data for sharks.

Species	K value	Reference
<i>Rhizoprionodon terraenovae</i>	0.35-0.50	Branstetter 1987
<i>Carcharhinus limbatus</i>	0.27	Branstetter 1987
<i>Isurus oxyrinchus</i>	0.20-0.27	Pratt and Casey 1983
<i>Prionace glauca</i>	0.22	Branstetter 1987
<i>Carcharhinus brevipinna</i>	0.21	Branstetter 1987
<i>Galeorhinus galeus</i>	0.16	Olsen 1984
<i>Carcharhinus leucas</i>	0.08	Branstetter and Stiles 1987
<i>Squalus acanthias</i>	0.05-0.07	Ketchen 1975
<i>Negaprion brevirostris</i>	0.06	Brown and Gruber 1988
<i>Carcharhinus plumbeus</i>	0.04-0.05	Casey et al. 1985

Despite problems encountered in determining consumption rate, it is apparent that sharks consume less on a percentage body weight basis than most teleosts. Many carnivorous teleosts consume 20-30% bw/d (Brett and Groves 1979), while the maximum ration voluntarily consumed by lemon sharks (growing ten times faster than wild sharks) is less than 3% bw/d (Gruber 1984).

Based on average body weights and estimates of daily ration, annual rate of consumption can be calculated for the lemon shark and several other species. When annual consumption is expressed as the number of times an equivalent of body weight is consumed, comparisons between sharks of different sizes are possible (Table 6). Also included in Table 6 are several estimates of annual consumption based on the energetic requirements for metabolism. The high level of annual consumption by mako sharks is consistent with greater energy requirements of this species, whereas the level of consumption by spiny dogfish, a cold water species with a low metabolic rate, is low (Brett and Blackburn 1978).

Production

Based on annual growth rates, annual production can be estimated for young sharks of several species. Again, for ease of comparison of species of different sizes, annual production for an individual is expressed as percentage

increase of initial body weight (Table 7). Rates of production of most teleosts, based on annual increases in body weight, are higher than that for elasmobranchs listed in Table 7. Many teleosts double their body weight in less than a week, which represents a tremendous weight increase on an annual basis (Brett and Groves 1979).

Other sharks appear to grow at faster rates than those shown in Table 7. Branstetter (1987, 1990) proposed that growth rates of sharks are correlated with the ecology of each species. Growth rates of sharks (lemon, bull, sandbar) that inhabit shallow bays and estuaries early in life are relatively slow. Other species such as Atlantic sharpnose, *Rhizoprionodon terraenovae*; spinner, *Carcharhinus brevipinna*; blacktip, *Carcharhinus limbatus*; and blue shark, have relatively rapid growth rates (Table 8). In these species, parturition occurs in offshore waters, making pups more susceptible to predation, thus favoring rapid growth in these environments. These life history traits may represent two different strategies for improving the survival rate of young. Although consumption has not been measured for fast-growing species, higher levels of growth may be dependent on increased levels of consumption.

Gross conversion efficiency (K_1) represents the efficiency of food conversion to growth (Brafeld and Llewellyn 1982). Using values obtained for daily ration and growth, we have calculated conversion efficiencies for several species of sharks on an annual basis (Table 9).

Table 9.
Estimates of gross conversion efficiency (K_1), the efficiency of food conversion to growth, for sharks on an annual basis.

Species	Annual production (kg)	Annual consumption (kg)	K_1	Reference
<i>Carcharhinus plumbeus</i>	1.066	7.56	14.1	Medved et al. 1988
<i>Negaprion brevirostris</i>	1.546	10.35-13.80	11.2-14.9	Cortes 1987
<i>Squalus acanthias</i>	0.031	0.51	5.9	Jones and Geen 1977

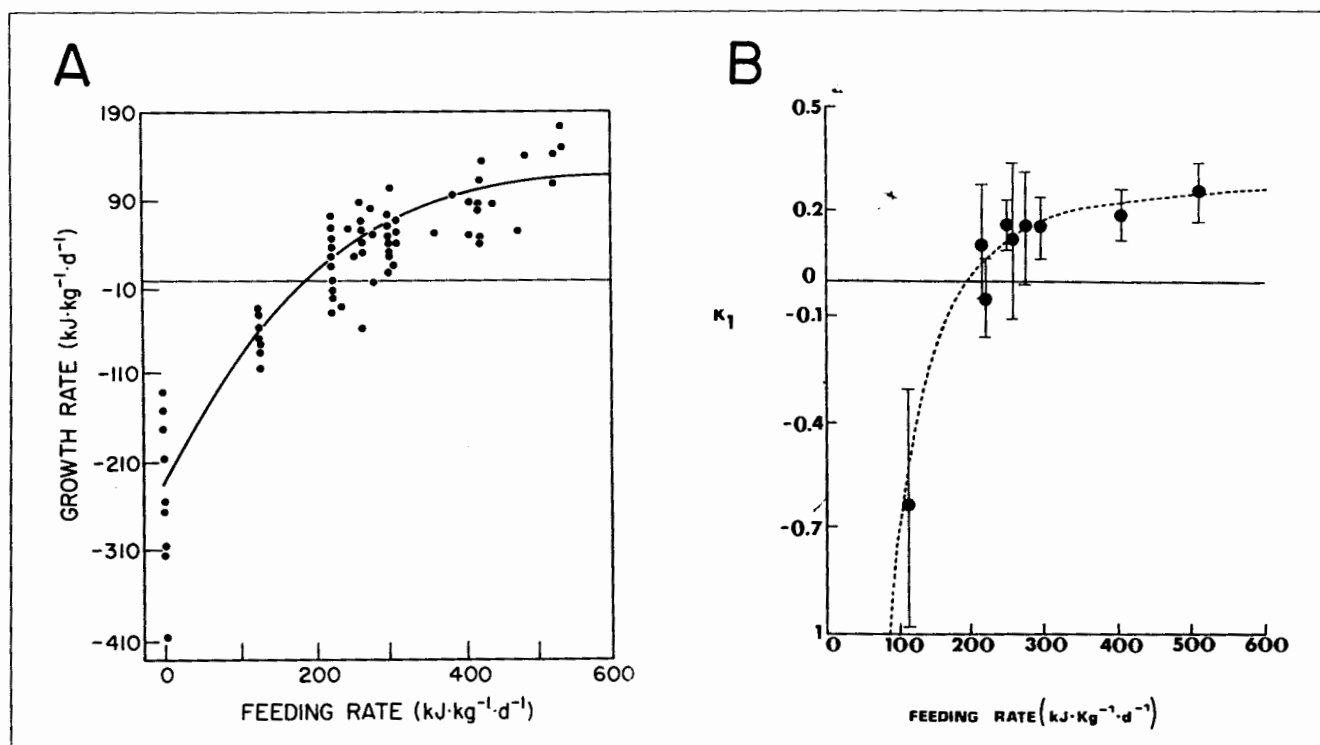


Figure 6.

A. Growth rates for young lemon sharks at 25°C as a function of feeding rate. (From Cortes 1987.) B. Gross conversion efficiencies for young lemon sharks at 25°C as a function of feeding rate. Circles are experimental means, vertical bars designate ± 1 SD. The best fitting curve was traced by eye. (From Cortes 1987.)

The considerable economic and biological importance of fish are incentives for attempting to understand more completely their rates of production (Gerking 1954). Since food supply is the major factor controlling production of most animals, understanding the relationship between food supply and growth is a necessity. Cortes (1987) conducted a series of experiments aimed at establishing the relation between feeding level and production in the juvenile lemon shark. Growth associated with various levels of energy intake were recorded and represented in terms of rate and efficiency (Figure 6, A and B). Cortes found that increasing intake and growth were directly correlated, but growth rate leveled off at high rations.

According to Brett et al. (1969), measurement of food conversion efficiency may well offer one of the greatest sources of insight concerning what governs the success of an animal. We have determined food conversion efficiency of lemon sharks, and found that it continues to increase with increased ration, eventually leveling off at high rations. At intake levels above maintenance, K_1 of the lemon shark is between 10 and 25, which is comparable to values reported for teleosts (Brett and Groves 1979). At the maximum ration voluntarily consumed, Cortes found growth rate and K_1 continued to increase. In several studies involving teleosts, K_1 peaks at an optimum feeding rate and decreases at intake levels beyond the optimum

(Paloheimo and Dickie 1966; Huisman 1976; Elliott 1982; Borgmann and Ralph 1985). Food is not converted to growth as efficiently at these high ration levels owing to factors such as increased activity, decreased absorption efficiency or increased metabolic costs of processing the additional food (Warren and Davis 1967). However, we were unable to induce young lemon sharks to voluntarily feed at intake levels high enough to yield lower growth efficiencies.

Laboratory measurements of growth and conversion efficiency for the lemon shark compare well with information obtained from the field. We were able to estimate the level of consumption required to support rate of field growth, as determined from tag and recapture data, from the growth curve for captive lemon sharks (Figure 6A). Daily ration in the field was estimated to be 1.5 to 2.0% bw/d, which corresponded well with estimates of daily ration obtained by analysis of stomach contents and rate of gastric evacuation (Table 4). Using the laboratory derived K_1 curve in Figure 6B, the K_1 expected for lemon sharks feeding at a rate comparable to the daily ration level was calculated. The generated values of 10–12 agree well with K_1 (11.2–14.9) calculated on an annual basis from field estimates of growth and consumption (Table 9). Thus, estimates of consumption and production in both the laboratory and the field are in agreement.

Growth does not appear to be limited by the ability of the lemon shark to absorb energy, or to convert consumed energy to growth. Experiments conducted by Bushnell (1982) showed that the lemon shark has a metabolic rate comparable to active teleost predators, indicating that metabolic costs were not unusually high. The major factor responsible for slow rates of growth observed in lemon sharks (Gruber and Stout 1983; Henningsen and Gruber, in prep.) is a relatively low level of consumption, which may in turn be limited by a slow rate of digestion.

Applying values of individual consumption and production to a population of lemon sharks in the field may be valuable in assessing the impact of this species on a local level. The population of juvenile lemon sharks inhabiting the north lagoon of Bimini, Bahamas has been estimated at approximately 87 individuals (Henningsen and Gruber, in prep.). An ecosystems modelling study has shown that this ecosystem can support about 250 juvenile lemon sharks (Jacobsen 1987). If these estimates are realistic, then competition between young lemon sharks may not be extreme in this habitat, and food may not be limiting. On the other hand, teleost and elasmobranch predators may compete heavily for food with the lemon sharks, and this competition may lead in turn to intense intraspecific competition.

Conclusions

The lemon shark is a member of the most speciose family of sharks (Carcharhinidae), and conclusions drawn about

many aspects of feeding, digestion, consumption, and production in this species may be applicable to many other species of sharks. Considering the number of species of sharks, and the variety of habitats occupied by different individuals, populations, and species, few generalizations are likely to hold for all sharks under all circumstances. Given the extreme variation in food types and prevailing environmental conditions which are selected by sharks, exceptions to generalizations are even more likely. As the number of species under investigation grows, and our understanding of the ecology of these animals improves, previous conclusions will be abandoned and new theories will be accepted. There are, however, several generalizations with respect to feeding ecology that may be appropriate: 1) Sharks are generally opportunistic feeders, able to use a variety of prey in a variety of habitats throughout the year; 2) Sharks may feed most heavily upon the most abundant prey item, opportunism and selectivity being modified by the availability of prey; 3) Feeding occurs in short bouts, followed by longer periods of digestion, when feeding is reduced; 4) Feeding is asynchronous and feeding periodicity has not been well established; 5) Time for complete gastric evacuation and for elimination of a meal from the digestive tracts of sharks is substantially longer than those of most teleosts; 6) Estimates of daily ration for sharks are lower than those for most teleosts; 7) Relative annual consumption and production is lower for sharks than for most teleosts; 8) The lemon shark (and presumably other species) is capable of absorbing and converting energy to growth with efficiencies comparable to those of teleosts.

Acknowledgments

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